ON MESARCH STRUCTURE IN LYCOPODIUM[1]

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(WITH PLATE X)

Halftone

The position of the protoxylem in relation to the later-formed elements of the wood has been the subject of careful investigation in the various groups of vascular plants, both fossil and living, and has often been brought forward as evidence of the relationship of one group to another.

In his description of the anatomy of a specimen of Sigillaria, in 1839, BRONGNIART (1) showed the central cylinder to be formed of a ring of vascular bundles, each composed of an inner, primary part, and an outer, secondary part, the latter characterized by the radial arrangement of its elements. The small spiral elements lie on the outer edge of the primary wood, which was all developed in a centripetal direction, while the secondary wood grew centrifugally. The protoxylem is thus surrounded by later-formed elements.

In his classic work on the anatomy of the cycads, METTENIUS (2), in 1861, described the structure of the vascular bundle in the petiole and blade of certain living cycads. He showed that in the leaf-trace, as it leaves the cylinder of the stem, the protoxylem is all on the inside of the later-formed, mostly secondary, wood, but that as the bundle ascends into the petiole, the later-formed wood gradually bends around inwardly and incloses the spiral elements. Finally the centrifugal wood, which is probably all secondary, is greatly reduced, and separated from the protoxylem by parenchyma, while the centripetal wood forms the bulk of the bundle, and bears at its outermost point the cluster of spiral tracheids. METTENIUS (2, p. 582) noticed the resemblance between this bundle and one of the stem bundles of Sigillaria, and remarks that the much greater development of centrifugal secondary wood in the latter is due to the fact that it belongs to the vascular system of the stem.

RENAULT (3), however, was the first to really suggest the affinity

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of the cycads with the Sigillariae on the basis of a common possession of this character.   He carefully distinguished the irregularly arranged centripetal wood from the radially disposed centrifugal wood of the sigillarian bundle, and was the first to describe the structure of the leaf-trace in this genus.   The elements in the leaf are also formed in two directions, those on the outside often being radially arranged.   This structure making the comparison with the cycads still closer, RENAULT comes to the conclusion (3, p. 281) that "les Cycadées actuelles qui possèdent dans la structure du cordon foliaire cette analogie si frappante avec certaines plantes houillères, n'en sont que les représentants amoindris et en voie de décadence."

RENAULT has applied the term diploxylic to bundles possessing centrifugal as well as centripetal wood, and has grouped together Sigillaria and Poroxylon under the head DIPLOXYLÉES.   Count SOLMS-LAUBACH (4, p. 263), however, called attention to the fact that where all the centrifugal wood is secondary, the original primary bundle, which thus has its oldest elements on the very outside, is of a different type from one where there is primary wood on the outside, as well as on the inside, of the protoxylem.   For the former type of primary bundle he suggested the name exarch, and for the latter type mesarch, terms which have since been in current use with those meanings.   RENAULT's diploxylic implies the presence of secondary wood.

On the characteristic possession of one of these two main types of primary bundle, modern writers have often divided living and fossil vascular cryptogams into two great groups—the Fern series generally, as typically mesarch, and the Lycopodiales, fossil and living, as typically exarch.

This general rule, however, does not hold at all closely.   Among living ferns, there are numerous instances of exarch structure, for example in the stem of *Trichomanes scandens*, of *Lygodium dichotomum*, and of *Loxoma Cunninghamii*.   The same holds true of fossil ferns and their allies.   Zygopteris shows both internal and external protoxylem, while Megaloxylon is clearly exarch.

Among the typically exarch forms, on the other hand, RENAULT (3) has figured mesarch leaf-traces in the Sigillariae.   They are also found in certain species of Lepidodendron.   Numerous cases of such development also occur in the modern relatives of this group.   In

the center of each stem bundle of Tmesipteris there is a cluster of initial elements, the breaking-down of which often results in the formation of a lacuna. Although the cylinder of the stem of Selaginella is characteristically exarch, GIBSON (5) has noted, in the case of the protostelic *S. spinosa*, that in the trailing portion of the stem, all the protoxylem is in the center of the cylinder, completely inclosed by metaxylem. The root in the whole genus is also distinctly mesarch. In Phylloglossum, it is well known that the tubular stele at the base of the peduncle, the ring of bundles into which this divides higher up, and the traces of the sporophylls, have their first-formed wood elements surrounded on all sides by later ones. Exarch development seems entirely lacking, both in this genus and in Tmesipteris.

In Lycopodium, however, precisely the reverse seems at first sight to be true, and I have been unable to find a recorded instance of the occurrence of mesarch development in the genus.

In an endeavor to determine the presence or absence of such a character, the following species and varieties of Lycopodium were investigated: *L. inundatum* L., and var. *Bigelovii* Tuckerm.; *L. lucidulum* Michx.; *L. annotinum* L.; *L. obscurum* L.; *L. tristachyum* Pursh; *L. complanatum* L. var. *flabelliforme* Fernald; and *L. clavatum* L.

L. inundatum and its variety are somewhat delicate forms, and have by far the most poorly developed vascular system of the species looked at. In both, the xylem rays are few in number (3–6), and along the much broadened end of each extends a row of crushed protoxylem elements. There is no indication of metaxylem outside of these. In the leaf-trace, however, especially at a little distance from the cylinder, the smaller elements, ringed or loosely spiral, tend to become clustered at the center of the bundle. Just before the trace enters the leaf, these elements break down, leaving a protoxylem lacuna, completely surrounded by later-formed, closely spiral elements. This is perfectly evident in both transverse and radial sections (*figs. 1, 2*).

In the case of *L. lucidulum*, the central cylinder is also small, in comparison to the diameter of the stem, and its xylem rays are few in number and broadened at the ends. As in *L. inundatum*, however, there is no indication of centrifugal wood in the cylinder itself, but the

leaf-traces, though composed of a comparatively small number of cells, show in nearly every case a mesarch structure (*fig. 3*).

The remaining species studied have much better developed vascular tissues. Their cylinders are in general very similar, being composed of a much larger number of xylem rays, which end more or less acutely. In all the species, metaxylem cells occur just outside the protoxylem of the cylinder. In *L. tristachyum* and *L. complanatum* var. *flabelliforme*, this mesarch development is not common, but in *L. obscurum* and *L. clavatum*, especially the latter, it is very noticeable. In vertical section, the centrifugal elements are seen to be reticulate, not scalariform, as in the rest of the metaxylem (*figs. 4, 6*). The exceptional development of this structure in *L. clavatum* may be due to the fact that its vegetative growth is more luxuriant than that of any of the other species studied. In all these forms, the leaf-trace again is very clearly mesarch (*figs. 7–9*). This is especially conspicuous, perhaps, in *L. tristachyum* and *L. complanatum* var. *flabelliforme*, where a large protoxylem lacuna occurs in the center of the trace (*fig. 9*).

In all the species, the leaf-trace, as it leaves the cylinder, is very small, but rapidly increases in size in the cortex, where it possibly serves to store water.

The development of the protoxylem of the central cylinder is always from without inward. The single row of centrifugal metaxylem elements occurs directly outside the earliest-formed xylem cells. Sections through the growing-point of *L. clavatum* showed that the metaxylem elements on both sides of the protoxylem developed nearly simultaneously. In the leaf-trace, also, as was shown by a very young stem of *L. complanatum* var. *flabelliforme*, the elements surrounding the protoxylem are all developed at the same time.

The leaf-trace of *Selaginella rupestris* (L.) Spring was investigated, and though composed of a very small number of cells, it showed a strong tendency toward mesarch arrangement. It is interesting to note here an observation of GIBSON (**6**, p. 151) on the leaf bundle of Selaginella. "In the upper third of the leaf the protoxylem elements become accompanied by several short reticulate tracheides which flank the spiral tracheides, and in section (e. g., of *S. Braunii*) may inclose the spiral elements completely."

It is noteworthy that in certain of the fossil Lycopodiales, as above mentioned, there is clear evidence of the possession of mesarch structure in the primary wood of the leaf-trace.

That there is no sharp line of cleavage between mesarch and exarch vascular cryptogams is thus perfectly clear. Among the main groups, we have numerous instances of both types of development, and the one merges, little by little, into the other. In Lycopodium, the centrifugal wood of the stem, when present, consists of only a few tracheids; in such forms as Lyginodendron, for instance, and in many ferns, the spiral elements are near the outside, while in Tmesipteris and Phylloglossum, they are in the very center. The variability of the position of the protoxylem in the primary wood bundle, and its consequent unreliability as a phylogenetic character, cannot be too strongly emphasized.

While the structure of the primary bundles of the vascular cryptogams cannot be used as a guide to their interrelationships, it furnishes an excellent character for the whole group, both living and fossil forms. The presence in the stem of *centripetal primary wood, continuous with the protoxylem,* is the distinguishing mark of these plants. The older French botanists appear to have been perfectly right in characterizing their *bois centripète* as cryptogamic wood, for the Sphenophyllales, Lycopodiales, and Filicales show this structure very clearly. The only apparent exception[2] to the rule is the calamitean series, including the modern Equisetales. A species of Calamites, however, the so-called *C. pettycurensis,* or Protocalamites, has recently been shown to have well-developed centripetal wood on the inner face of the protoxylem canals of the stem (SCOTT 7). Further, EAMES (10), working in this laboratory, has distinguished a mesarch condition, with consequent presence of centripetal xylem, in the traces of the vegetative and reproductive leaves of several living species of Equisetum. It thus seems certain that centripetal wood was once well developed in the Calamites and their allies, but in the process of time has been almost entirely lost.

It is worthy of note that though secondary wood is often present in the vascular cryptogams, and may constitute the bulk of the central cylinder, the protoxylem is intimately associated with the centrip-

[2] Exclusive of that aberrant group of ferns, the Ophioglossales.

etal primary wood.   In the higher plants, the centrifugal xylem preponderates, and the protoxylem becomes continuous with it, even in the cases where centripetal elements are present.   The only exceptions to this rule occur in foliar bundles.   The leaves of living cycads and of the Cordiates show true cryptogamic wood in their vascular strands, with the protoxylem closely associated with it, though in all cases centrifugal secondary wood is present.   This persistence of a cryptogamic structure in the leaf, among the higher plants, furnishes good evidence of the conservatism of the foliar bundle.   Scattered centripetal elements appear in the peduncle of certain cycads and in the cotyledons of Ginkgo, also seats of vestigial characters, and centripetal wood is fairly well developed in the leaf of Prepinus (JEFFREY **9**) and in the stems of many of the Cycadofilices; but in all these cases, the bundle is of the higher type, the protoxylem being continuous with the *centrifugal* wood.

The structure of the vegetative stem, of the floral axis, and of the leaf, in certain living Cycadaceae, shows clearly the transition from the lower type of wood to the higher.   In the stem, the protoxylem joins the centrifugal wood and there are no centripetal tracheids.   In the stalk of the male cone of *Stangeria paradoxa*, and to a less extent in the male and female peduncles of three other species of cycads, as shown by SCOTT (**8**), scattering centripetal xylem elements are present. They are not connected with the protoxylem, however, but are separated by parenchyma from the rest of the bundle, which otherwise is exactly similar to those found in the stem.   In the petiole and blade of the cycad leaf, however, there is more than this faint suggestion of ancestral structures; for here, as above described, true cryptogamic wood occurs, consisting of well-developed centripetal elements directly continuous with the protoxylem.   In the petiole, and sometimes in the blade, centrifugal wood is present as well.   This is separated by parenchyma from the protoxylem, and appears to be largely, if not entirely, laid down by cambial activity.   Its resemblance to a sigillarian bundle, as noted by RENAULT, is thus pretty exact.   SCOTT, however, believes that some, at least, of the centrifugal wood is primary, and consequently that true mesarch development takes place, a condition which he compares to that found in the stem bundles of *Lyginodendron Oldhamium*.   He presents the mesarch structure

of the peduncle and of the leaf as evidence of the affinity of modern cycads to the fossil Lyginodendreae and Poroxyleae. While the conclusion as to affinities is very probably correct, the argument is not entirely convincing. The cryptogamic ancestry of the cycads is proven, but that is all; for we have already seen that the possession of mesarch primary wood is limited to no one group of plants, and that its presence or absence is of no value as phylogenetic evidence.

CONCLUSIONS

The position of the protoxylem in the primary wood bundle of vascular cryptogams is very variable, for in all of the groups it may be almost anywhere in the strand. It is consequently of little value in determining the relationship of any group to other groups or to the higher plants. A constant primitive feature in the vascular cryptogams, however, is the presence in the stem of cryptogamic wood—centripetal xylem continuous with the protoxylem elements. Whenever such a feature occurs in any of the higher plants, it can be used as evidence in tracing their affinity only with vascular cryptogams in general, not with any particular group of them.

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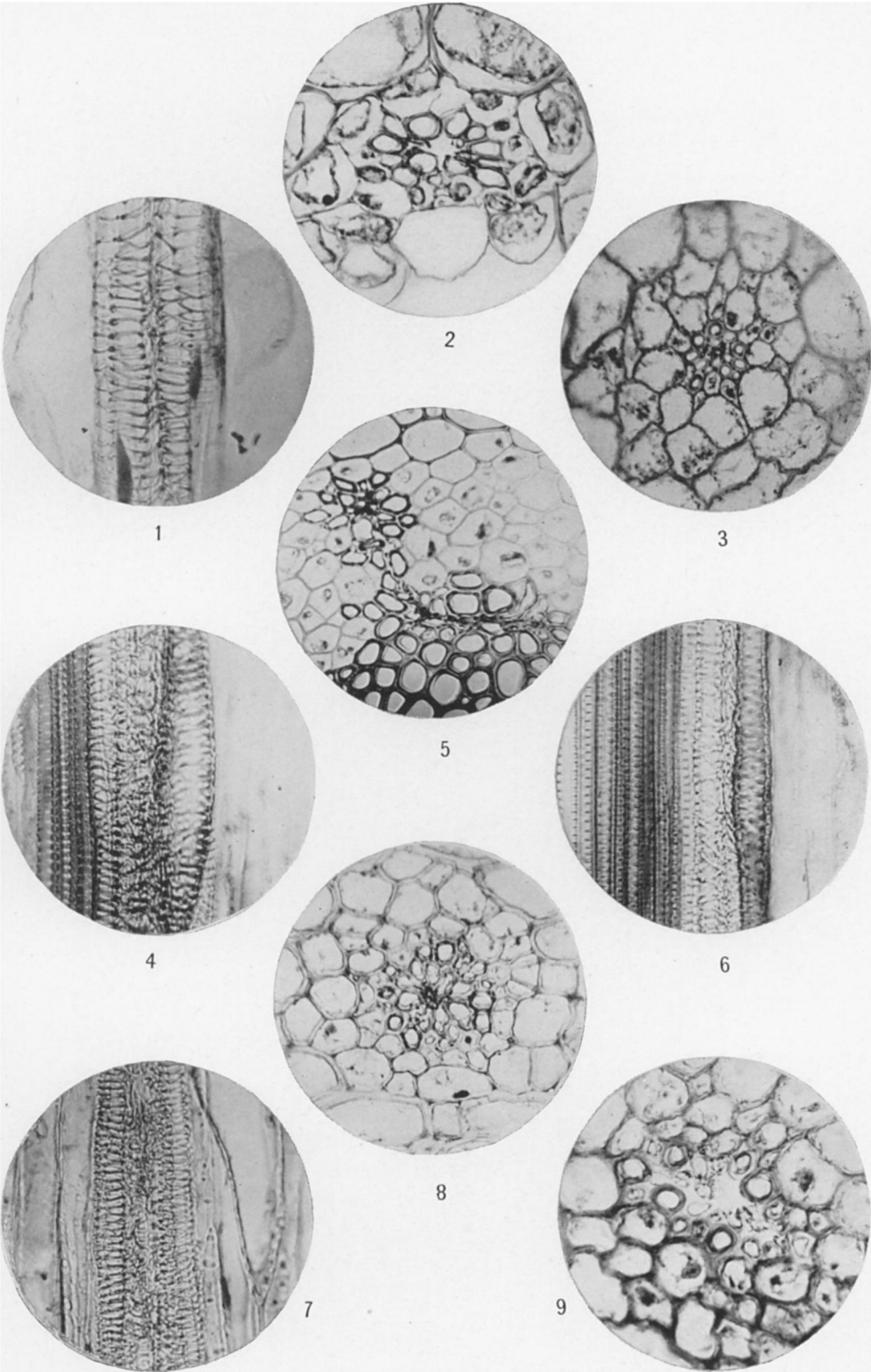
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EXPLANATION OF PLATE X

FIG. 1.—*Lycopodium inundatum* var. *Bigelovii;* longitudinal radial section through a leaf-trace. ×500.

FIG. 2.—*Lycopodium inundatum* var. *Bigelovii;* transverse section of a leaf-trace near the margin of a mucilage cavity. ×500.

FIG. 3.—*Lycopodium lucidulum;* transverse section of a leaf-trace. ×500.

FIG. 4.—*Lycopodium clavatum,* longitudinal radial section through the margin of the central cylinder, showing the single centrifugal metaxylem element on the right. ×500.

FIG. 5.—*Lycopodium clavatum;* transverse section through the margin of the central cylinder at the point of departure of a leaf-trace; the dark line of crushed cells marks the position of the protoxylem. ×500.

FIG. 6.—*Lycopodium obscurum;* longitudinal radial section through the margin of the central cylinder, showing centrifugal metaxylem as in *fig. 4.* ×500.

FIG. 7.—*Lycopodium clavatum;* longitudinal radial section through a leaf-trace. ×500.

FIG. 8.—*Lycopodium clavatum;* transverse section of a leaf-trace. ×500.

FIG. 9.—*Lycopodium tristachyum*; transverse section of a leaf-trace. ×500.